Triodia caelestialis (Triodieae: Chloridoideae: Poaceae), a new species from the central Kimberley, Western Australia

G Armstrong

School of Environmental Research, Charles Darwin University,
Darwin NT 0909
Current address: Mornington Wildlife Sanctuary, PMB 925,
Derby WA 6728

graeme.armstrong@students.cdu.edu.au

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Abstract

Triodia caelestialis G. Armstrong, a new species from the central Kimberley of north-western Australia is described based upon morphological characters and reproductive traits. The taxon is distinguished from its sister species *T. acutispicula* Laza. by differences in inflorescence morphology and allocation of resources to sexual reproduction. *T. caelestialis* produces approximately five times more seed than *T. acutispicula* resulting in higher seedling densities and does not produce stolons whereas *T. acutispicula* allocates greater resources to asexual reproduction through the production of numerous stolons. A predicted species range map is produced using BIOCLIM modeling and the morphological effect of a leaf axil fungal infection is discussed.

Keywords: Triodia, Poaceae, Kimberley, BIOCLIM

Introduction

During the course of research into the reproductive strategies of *Triodia* species at Mornington Wildlife Sanctuary, in the central Kimberley, it became apparent that specimens identified as *T. acutispicula* Laza. may not have constituted a single taxon. All individuals in populations identified as *T. acutispicula* share the same unusual floret morphology, described here for the first time; however, some individuals are highly stoloniferous while others produce no stolons. Based on the premise that this difference in allocation of resources to reproduction indicated a taxonomic difference data were collected on the morphology and reproductive strategies of the two morphotypes to determine if a taxonomic reassessment was warranted.

Previous taxonomic work on Triodia by Mant et al. (2005), using molecular data, resolved a clade of 'soft' leaved species, those with a central row of stomata on the abaxial surface, to be nested within the 'hard' leaved species of Triodia. Though differing from previous infrageneric groupings based on floral and leaf anatomy (Lazarides 1997), this classification did not dispute previous species definitions based on the same data sets. It would not be unreasonable therefore, to assume taxa within the 'soft' clade sharing similar floral characteristics be assigned as sister species. The two morphotypes of interest in this research share 'soft' leaves and the same unusual floret morphology suggesting sister species status, thus allowing a direct comparison between them. Growing sympatrically suggests observed differences are due to genetic, not environmental factors and the use of both morphological and reproductive data provides a good basis for this taxonomic reassessment.

In determining the specific status of T. caelestialis morphological characters were considered along with comparative reproductive traits of its sister species T. acutispicula. Morphological descriptions and measurements are based on fresh samples collected at locations at Mornington Wildlife Sanctuary and 'Mt. House' Station. Reproductive data were collected on populations of both taxa at Mornington Wildlife Sanctuary. Specimens of T. caelestialis have also been observed in the King Leopold Ranges Conservation Park. Coordinates for these locations are in Table 1. The following T. acutispicula herbarium specimens were examined to identify possible specimens of T. caelestialis thereby identifying further localities for the latter, Perth 00486442, Perth 00486469, Perth 00879274, Perth 00486426, Perth 06960170, Perth 02384035, Perth 00486515 and AD96127037.

Table 1

Location names and coordinates (GDA 94) of specimens of *T. caelestialis* collected and observed.

Location	Coordinates	
Mornington Wildlife Sanctuary		
Research Centre		126°6.530'E
Boundary Pool		126°5.404'E
Sir John Gorge	17°31.181'S	126°12.791'E
Narrie Range	17°24.938'S	126°13.244′E
Mt. House	17°05.098'S	125°47.304'E
King Leopold Ranges Conservation	17°06.930'S	125°10.037′E

Methods

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Reproductive traits were recorded from observation of flowering times and quantifying reproductive allocation to stolon and seed production and seed to floret ratios at the 'Research Centre' populations of T. acutispicula (17°30.489'S 126°6.317'E) and T. caelestialis (17°30.445'S 126°5.804'E). Within both of these populations five 5 x 5 m quadrats were placed semi-randomly at least 5 m apart. Quadrats were selected as the nearest patch of uniform Triodia located at a right angle to a 20 m transect at each 5 m interval. Distances from the transect ranged from 0 to 10 m due to either patches of bare ground or the presence of trees. Within each quadrat stolons were quantified by allocation to one of the following categories; 0-25, 26-50, 51-75, 76-100 and >100. Stolon number was estimated in categories due to the inability of distinguishing a true stoloniferous shoot, which forms an independent ramet, from a young side branch. The number of seedlings from the current season were also counted within each quadrat. Seedlings were identified by being less than 10 cm tall and lacking an established root base. These counts were conducted on 16th June 2008. Seed number and seed to floret ratio were determined by counting the number of reproductive culms in a 1 x 1m quadrat within the first quadrat, counting the number of spikelets on a subsample of 10 randomly selected culms, and counting the number of fertile florets and full caryopses of 70 spikelets. This quadrat was selected subjectively as representing an average culm density within the first 5×5 m quadrat. These counts were made in February 2008.

Seed and floret counts were non-normal and of unequal variance and were therefore compared using the paired samples Wilcoxon test in Programme R http://www.r-project.org/.

The predicted species range map was prepared using the Biomap function in BIOCLIM 5.1 (Houlder *et al.* 2008) http://cres.anu.edu/outputs/anuclim.html), and intersecting this with sandstone habitat. Input data for Biomap were location and height data of known samples and Geoscience Australia 9 Second DEM Version 2.1. The distribution of sandstone was determined from Australian 1:250,000 Geological Series maps.

Choosing the bioclimatic variables to include in the model was based on assumptions regarding the most biologically meaningful variables and experimentation to look at the outcomes of combinations of variables. Using too many or too few variables either over-fits or underfits the model resulting in a predicted range across the entire north of the country or only encompassing the known localities. Many variables had little or no effect and it was found that using only 'Precipitation of wettest period' and 'Precipitation Seasonality' at full range produced a map that appears a realistic compromise between the possible extremes.

Taxonomy

Triodia caelestialis G. Armstrong, sp. nov.

Planta caespitosa, nec resinosa nec stolonifera, 40 cm alta \times 60 cm lata. Foliorum laminae flexuosae et torsivae ad 30 cm \times 2 mm. Culmi reproductivi 160 (> 200) cm alti \times 4–5 mm lati. Inflorescentia panicula in maturitate

aperta, 18–40 cm (plerunque 30 cm) longa, ramis primariis 11–26. Pedicelli spicularum lateralium 2–5 mm longarum compositi; spiculae terminalis pedicello ad 1.5 cm longo. Spiculae in quoque ramo usque 14 lineares, teres plerunque apice campanulato globum facientes. Flosculi 6–10, illis 1–3 basi fertibus, 0–2 caryopsibus in quoque spicula. Glumae 15–24 mm, linearo lanceolatae, glabrae, acuminatae, nervis 6–12. Lemma 5–7 mm longum, glabrum praeter seriebus paralellis pilorum adpressorum in quoque latere cristae angustae in dimidio indurato; lobi et aristae terni, lobis et aristis lateralibus 6–11, lobo et arista mediis 10–12 mm longis. Palea 0.6 cm longa. Callus 1–2 mm longus pilis lateralibus densis adpressis obtectus. Caryopsis 3 mm longa anguste oborata.

T: Mornington Wildlife Sanctuary Research Centre, central Kimberley, W.A. 17°30.627'S 126°6.530'E 21st January 2008 G. Armstrong holo: PERTH 07842791; iso: CANB, NT.

Caespitose, non-resinous, non-stoloniferous perennial forming compact, non-branching tussocks 40 cm tall x 60 cm wide. Non-reproductive culms to 4 cm long, found only within the basal leaf sheaths*, therefore not hummock forming. Leaf blades originating predominantly from within the basal sheaths; flexuose and spiraling, to 30 cm x 2 mm, slightly pungent; abaxial surface nerved in the median band and nerveless to margin, 'soft'; leaf orifice with hairs to 4 mm; ligule a membrane with cilia to 1mm total length, membrane 1/3 the length of the cilia. Reproductive culms smooth, 160->200 cm tall x 4-5 mm wide, with 3-5 prominent nodes to 6 mm diameter, often red on, above and below the node for c. 5 mm. Culm leaf sheath smooth, less than 1/2 internode length differing from basal leaves by ligule membrane being 1/4 the length of the cilia and leaves being very pungent. Inflorescence a panicle, contracted when immature, open at maturity, 18-40 (average 30) cm long with 11-26 primary branches with secondary branching of the basal branches; lower panicle branch 6-19 (average 10) cm long; rachis 0.5-1.5 mm diam.; branches and pedicels scabrous; simple hairs to 0.5 mm long sometimes on the sides of the branches at the axil; pulvinus commonly found on the inner side of the panicle branch at the axil forming a yellow crenulate surface, to 2 mm long, often growing beyond the outer edges of the branch. Pedicels of lateral spikelets of similar length, 2-5 mm long; terminal spikelet pedicel longer than laterals, to 15 mm long; hairs to 1 mm long sometimes present at pedicel axis. Spikelets up to 14 per branch; linear, terete, commonly with campanulate apex, forming a ball when dry. Florets 6-10, the basal 1-3 florets fertile with 0-2 caryopsis per spikelet, the apical 5-7 florets infertile, contiguous, consisting of only the lemma lobes, the middle 2 or 3 of these florets with wider lemma lobes than those below or above and having minimal distance between them on the rachilla flare at this point into a star shape; the lobes of these florets range from purple to straw-coloured, contrasting with the bright green nerves running up the centre of the lobe; uppermost florets reduced to awns (Fig. 2A). Glumes longer than spikelet without awns; +/- equal length, 15-24 mm, linear-lanceolate, scarious, glabrous, acuminate,

^{*} see note under fungal infection

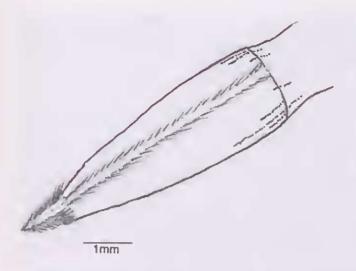


Figure 1. Lemma with 2 parallel rows of hairs running up the centre of the lower half. This contrasts with the glabrous lemma of *T. acutispicuta* Lazarides (1997) Fig. 10.

6–16 nerved in lower half, reduced to at least 3 in upper half, outer surface grading from smooth at base to asperulous above. Lemmas 5-7 mm long excluding lobes and callus, bitextured, indurate below, cartilaginous above with a hard thickening at the demarcation line on the inner surface 1-4 mm below sinus of lobes, often enclosing the edges of the palea, glabrous apart from two parallel rows of adpressed hairs either side of a narrow ridge, running up the centre of the lower indurate half (Fig. 1); lower indurate half of lemma often brown when mature which does not indicate the presence of a caryopsis; 3 lobes and awns with lateral awns shorter than mid-awn, mid-lobe and awn 10-12 mm long, lateral lobes and awns 6-11 mm; awns twisted and recurved, 3 nerved. Rachilla 3 mm long. Palea 6 mm long, bitextured, cartilagenous in the lower 3/4, hyaline in the upper 1/4, narrowly oblong, emarginate apex; keel margin ciliate, flaps hyaline. Callus 1-2 mm long, lateral dense adpressed hairs to 0.5 mm long, tip glabrous, sometimes curved, pungent. Caryopsis 3 mm long narrowly obovate, shallow groove lengthwise along inner side.

Distribution and Habitat. Specimens have been collected and observed in the central Kimberley region on Mornington Wildlife Sanctuary, 'Mt. House' Station and King Leopold Ranges Conservation Park. The herbarium specimens Perth 00486515 and Perth 02384035 have been identified as T. caelestialis extending the known range of T. caelestialis to "NE side of CRA camp, Ellendale, 24.3km from Gibb River Road 17°30'S 124°50'E" and "Charnely River Crossing, 55km Nth Beverley Springs 16°43'S 125°27'E" respectively. The coordinates given for Perth 02384035 refer to Beverley Springs Homestead and the actual site 55km north of this point would be located at approximately 16°13'S 125°27.4'E. Populations range from a few dozen individuals to several hectares, predominantly on quartzite sandstone pediment along the edge of a range or isolated outcrop, extending marginally onto the surrounding depositional sand (Fig. 2B). In the sandy areas stands of T. caelestialis and T. acutispicula abut and intermix at their margins. T. epactia stands abut those of T. caelestialis on the upward slope of sandstone ranges. A population grows on shale on Mt. House Station. This population abuts *T. aeria*.

Etymology. Alluding to the star shaped cluster of infertile florets at the apex of the spikelet; caelestialis: heavenly body, star.

Distinguishing characters. Current keys for identifying Triodia species are adequate to place *T. caelestialis* in *T. acutispicula* with some minor adjustments. In Lazarides (1997) the character of "plants resinous" at 4A must be ignored while accepting "blade on the lower (abaxial) surface strongly nerved or grooved in a median band". This is corrected in Lazarides *et al.* (2005). Sharp and Simon (2002) also places *T. caelestialis* successfully in *T. acutispicula* providing one of the final characters "culms to 1.5m tall" is treated as conservative.

T. caelestialis is distinguished from its closest relative T. acutispicula by the absence of stolons and exposed non-reproductive culms. Taller mean (160 cm vs. 140 cm) and maximum (>200 cm vs. 170 cm) reproductive culms in T. caelestialis and greater number of panicle branches (26 vs. 13) and spikelets per branch (14 vs. 7). The lemma of T. caelestialis has 2 parallel rows of hairs on the back of the lemma while the lemma of T. acutispicula is glabrous. The hairs at the leaf orifice are longer in T. caelestialis (4 mm vs. 1.5 mm) and the ligule is longer in total length (1 vs. 0.5 mm) and proportionally different with the membrane 1/3 the length of the cilia vs. equal length.

Phenology. Specimens of *T. caelestialis* at all localities within Mornington Wildlife Sanctuary flowered over a period of approximately 6 weeks from late January to the middle of March 2008. Specimens observed at 'Mt. House' Station and King Leopold Ranges National Park in late March 2008 retained reproductive culms but had lost all florets suggesting a similar flowering period. Specimens at the type locality were burnt in October 2006, regrew and flowered during January to March 2007.

Results of Reproductive Trait Analysis. The average number of seeds per floret is significantly greater in T. acutispicula at 0.8 than T. caelestialis at 0.53 (V = 503, p= 0.004), there is no significant difference between the number of fertile florets per spikelet, 2.5 to 2.4 (V = 234, p= 0.07) but there is significantly more spikelets per culm, 106 to 27.9 (V= 0, p-value = 0.005) and culms per m², 184 to 87.4 (V = 1, p= 0.003) in T. caelestialis than T. acutispicula. This results in a much greater number of seeds per m² in *T. caelestialis*, 10,337 compared with 1,950 in T. acutispicula. The ratio of seeds to florets is similar at 1:4.7 and 1:3 for T. caelestialis and T. acutispicula respectively. The mean number and standard deviation of seedlings in 5 x 5 m plots at approx. 4 months age for T. caelestialis was 28 (SD=25) compared with a mean of 0.2 (SD=0.45) for T. acutispicula. No stolons were recorded in T. caelestialis plots while T. acutispicula plots contained a mean of 85 (SD=20).

The lack of stolons in *T. caelestialis* reflects resource partitioning into a direct reproductive trait, however, the taxon shows limited vegetative reproduction through the separation of parts after senescence of the centre of the plant (Fig. 2D).

Predicted range. The range predicted for *T. caelestialis* from the BIOCLIM model shows a continuous band from

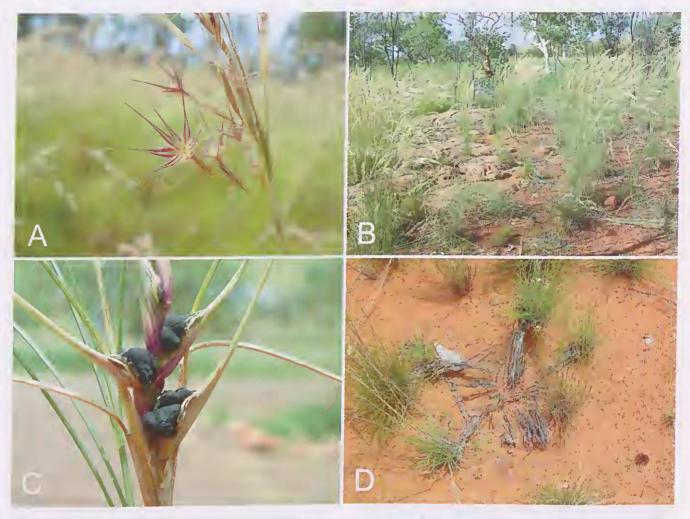


Figure 2. Photographs of *T. caetestialis*. A – florets showing star structure; B – habit and usual habitat; C – fungal infection in leaf axils; D – division of adult plant.

the Dampier Peninsula following the King Leopold Ranges across to Mornington in the east. Two outlying populations are predicted, one south of Wyndam and the other further east into the Victoria River district in the Northern Territory. No specimens of either T. caelestialis or T. acutispicula have been collected from the Northern Territory to support this prediction. The disjunction between the western and eastern Kimberley populations is also treated as an artifact due to the small sample size in the model and it is assumed these populations are joined. Removing the Dampier Peninsula due to lack of suitable sandstone habitat gives a predicted range following the King Leopold Ranges in a curve around the bottom of the Kimberley. (Fig. 3). The error in the model must be acknowledged and it is deemed biologically reasonable to assume the actual range may extend north into areas of higher precipitation.

Fungal infection. Individuals of both *T. acutispicula* and *T. caelestialis* show fungal infection in leaf axils, identified as the ergot *Claviceps* sp. in *T. acutispicula* PERTH 00879274. However, a diagram of the Ascostromata *Nigrocornus scleroticus* on *T. epactia* in Ryley (2003) has the same appearance as those found on *T. acutispicula* and *T. caelestialis*. When this fungal infection occurs on *T. caelestialis* the non-reproductive culms elongate and

appear externally as in *T. acutispicula*. Clay (1988) hypothsised that the close association of fungal hyphae with rapidly dividing plant cells would enhance the ability of the fungus to gain nutrient from the host plant while influencing plant growth through the release of phytohormones. This may explain the unusual elongation of non-reproductive culms in infected *T. caelestialis* (Fig. 2C).

Discussion

Morphological data alone distinguishes *T. caelestialis* from other *Triodia* species including its sister species *T. acutispicula*. However, this data only provides a pattern from which to derive a taxonomic delimitation which has no need of either a species definition or speciation process (Harrison 1998). The use of ecological data, in this case reproductive traits, allows the utilisation of information regarding the processes which are acting and have acted to unify a group of individuals and distinguish them from others. The reproductive traits, acting as multiple covarying characters, are a usable unified taxonomic character. The extent to which resources are devoted to sexual or asexual reproduction through seed density, floret number and stolon presence

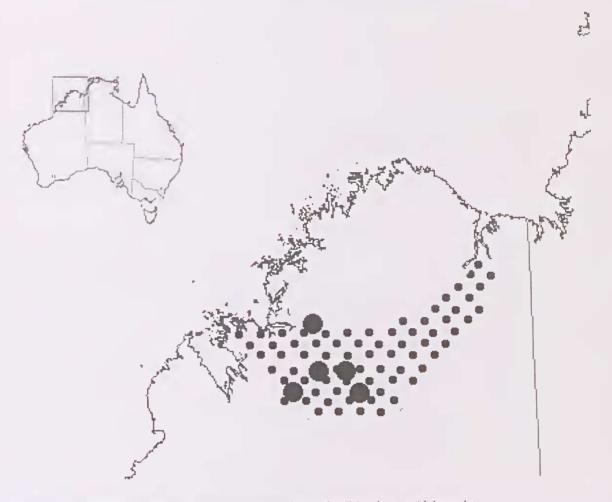


Figure 3. Predicted distribution range shown with small dots and known localities shown with large dots.

differs between the two related taxa and are taken to be the consequences of divergent evolution. Growing sympatrically reaffirms the genetic basis for this conclusion. The delimitation is therefore, given extra rigour through the use of the ecological data which reveals evolutionary processess. This conclusion provides a useful position from which to begin studies of speciation in *Triodia*.

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References

Clay K 1988 Clavicipitaceous fungal endophytes of grasses: coevolution and the change from parasitism to mutualism. *In*: Coevolution of Fungi with Plants and Animals (eds K A Pirozynski and D L Hawksworth). Academic Press, London. 79–105.

Harrison R G 1998 Linking Evolutionary Pattern and Process: The Relevance of Species Concepts for the Study of Speciation. *In*: Endless Forms: Species and Speciation (eds D J Howard and S H Berlocher). Oxford University Press, USA. 19–31.

Houlder D, Hutchinson M, Nix H & McMahon J 2008 AUNCLIM User's Guide, Version 5.1. Canberra: Centre for Resource and Environmental Studies, Australian National University.

Lazarides M 1997 A Revision of *Triodia* including Plectrachne (Poaceae, Eragrostideae, Triodiinae). Australian Systematic Botany 10: 381–489.

Lazarides M, Weiller C M & McCusker A 2005 Triodia. In: Flora of Australia: Vol. 44B (ed K Mallet). CSIRO Publishing, Melbourne, 203–255.

Mant R J, Bayer M D, Crisp M D & Trueman J W H 2000 A Phylogeny of Triodieae (Poaceae: Chloridoideae) based on the ITS Region of nrDNA: Testing Conflict between Anatomical and Inflorescence Characters. *In*: Grasses: Systematics and Evolution (eds S W L Jacobs and J Everett). CSIRO Publishing, Melbourne 213–217.

Ryley M J 2003 Nigrocornus sclerolicus, a Common Old World Balansioid Fungus In: Clavicipitalean Fungi: Evolutionary Biology, Chemistry, Biocontrol and Cultural Impacts, Mycology Vol. 19. (ed J F White Jr, C W Bacon, N L Hywell-Jones and J W Spatafora). CRC Press, USA. 247–271.

Sharp D & Simon B K 2002 AusGrass: Grasses of Australia. CD-ROM Version 1. Australian Biological Resources Study, Canberra, and Environmental Protection Agency, Queensland.